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Survey of Subalpine Understory Vascular Plant Communities in the face of Spruce Beetle Disturbance

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SURVEY OF SUBALPINE UNDERSTORY VASCULAR PLANT COMMUNITIES IN THE FACE OF SPRUCE BEETLE DISTURBANCE

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SURVEY OF SUBALPINE UNDERSTORY VASCULAR PLANT COMMUNITIES IN THE FACE OF SPRUCE BEETLE DISTURBANCE

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Abstract

Spruce beetles (*Dendroctonus rufipennis*) parasitize Engelmann spruce trees (*Picea engelmannii*) which grow in subalpine forests between 9,000 and 11,500 feet (2,743 to 3,505 meters). These beetles are endemic to Colorado and traditionally contribute to forest renewal and succession; however, warming annual temperatures have increased beetle populations and stressed subalpine trees making the latter susceptible to a greater severity of infection. We predicted that spruce beetle disturbance would increase the available sunlight and nutrients to surrounding understory vegetation, slowly increasing understory species diversity of the area. To test this, we surveyed understory vascular plants from forty-four plots in subalpine forests using a chronosequence of over 20 years of spruce beetle infestation. We recorded 128 species across all age classes, the most common of which were *Vaccinium scoparium* (Kinnickinick), *Abies bifolia* (Subalpine fir), *Picea engelmannii* (Engelmann spruce), *Arnica cordifolia* (Heartleaf arnica), and *Chamerion angustifolium* (Fireweed). We also noted lower diversity in the recently affected plots and higher diversity in the plots affected over 14 years ago. Overall, our data suggest that vascular understory vegetation diversity increases slowly after spruce beetle infestation, however the presence of spruce saplings across the study area may indicate future spruce-fir forest regeneration in disturbed areas.

Acknowledgments

I would like to thank Dr. Emily Holt first and foremost for her persistence, inspiration, and guidance throughout this project. Special thanks to our fearless leader: Anna Freundlich, and her sister Lilian Freundlich. Much appreciation goes to Mikaela Cain, Danielle Higashi, Dr. Mitt McGlaughlin, the UNC Biology Department, and the Center for Honors, Scholars, and Leadership.

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Introduction

Between 1997 and 2010, spruce and mountain pine beetles (*Dendoctonus rufipennis*, *D. ponderosae*, respectively) destroyed over 5 million hectares (50,000 km^2) of western US forests (Bentz & Klepzig 2014). This mass destruction is a consequence of their irruptive population growth, due in part to severe droughts, warming temperatures, and increased blowdown (Bentz et al. 2010, Bentz & Klepzig 2014). Drought reduces the vigor and energy reserves of host trees, increasing their susceptibility to attack, while warm temperatures can increase the production of yearly broods (Hart et al. 2014, Shebeck et al. 2017). Finally, because spruce beetles generally prefer fallen host trees to living ones, large storms may provide more blowdown to influence local population booms (DeRose & Long 2012, Schebeck et al. 2017). The effects of these factors will intensify with warming global temperatures potentially leading to more outbreaks in the future (Hart et al. 2014) According to the Report on the Health of Colorado's Forests (2018), 40% of the state's subalpine forests have been affected by spruce beetles, which have been considered "the most widespread and destructive forest insect pest" since 2011.

Changes in understory composition after a spruce beetle attack can predict forest regeneration (Fornwalt et al. 2018). In mature stands, large spruce and fir trees will use most of the available light and nutrients, which may be released after spruce beetle disturbance. Others have observed changes in the understory community as sedges, shrubs, and graminoids abound after beetle-kill (Zorio et al. 2016). However, these changes vary with location based on the initial forest characteristics and overstory composition (Boucher & Mead 2006). Understory plant development has been used as a proxy to measure the ecological health of a forest (Boucher & Mead 2006, Kreyling et al. 2008a, Kreyling et al. 2008b, Fornwalt et al. 2018). In studies investigating other disturbance types, changes are the most drastic immediately after fire, clearcutting, and salvage logging operations, most likely due to the sudden decrease in basal area and canopy; under these circumstances, community regeneration may take years to reach its original state (DeRose & Long 2012, Kreyling et al. 2008a, Fornwalt et al. 2018).

We consider the effects of spruce beetle outbreak as more subtle than fire or logging, which may take longer to change the understory community. Infested spruce trees lose their needles over the course of two years and may fall down the following year from severe summer storms (Holsten et al. 1999). Shifts in the understory community often are not apparent until decades after infestation, and transitional phases may persist until the area develops into a mature forest again (Winter et al. 2015). For this reason, it is important to continue studying spruce beetle outbreaks for many years after the initial outbreak. We consider the understory composition of northern Colorado subalpine forests that have been previously affected by spruce beetles over a span of 21 years, and predict that understory species presence and diversity will increase due to released light and nutrients from dead spruce trees. Our goals are to (1) describe understory species across all plots in our study area, (2) describe environmental characteristics of every plot, and (3) determine if a pattern exists between spruce beetle disturbance and understory growth.

Methods

Our study area occurred within two National Forests (NF): the Roosevelt NF, located to the east of the Continental Divide in north-central Colorado; and the Routt NF, located in north-western Colorado (106.8527778 - 105.4532623° W, 40.9932959 - 40.4963906° N; Figure 1). The study area spanned parts of Larimer, Boulder, Jackson, and Routt counties. The elevation of our study area ranged between 8,894 and 11,066 feet (2,711 to 3,373 meters). We used aerial imagery of the study area from the Colorado State Forest Service Aerial Tree Survey from 1996 to 2017 (CSFS & U.S. Forest Service Rocky Mountain Region 1996 – 2017). These surveys give geospatial information about infested acreage of Colorado by year.

One of the goals of our study was to investigate vegetation changes over time using a chronosequence approach; we used these data to construct four age classes and one undisturbed class categorizing changes since beetle infestation. Age classes were divided into five groups of similar size (average 6.9 acres, standard deviation 2.7 acres) rather than time span, which explains the varying lengths of time for each class, i.e. class 1 spans eight years, class 2 spans two years, class 3 spans four years, class 4 spans five years, and class 5 spans seven years (Table 1). ArcMap10.6.1 was used to merge yearly data into our age classes, and then randomly generate 20 points per class, or 100 total points. Before field work began, we selected a total 44 of these points as priority based on accessibility and visited each one once between May and August 2018.

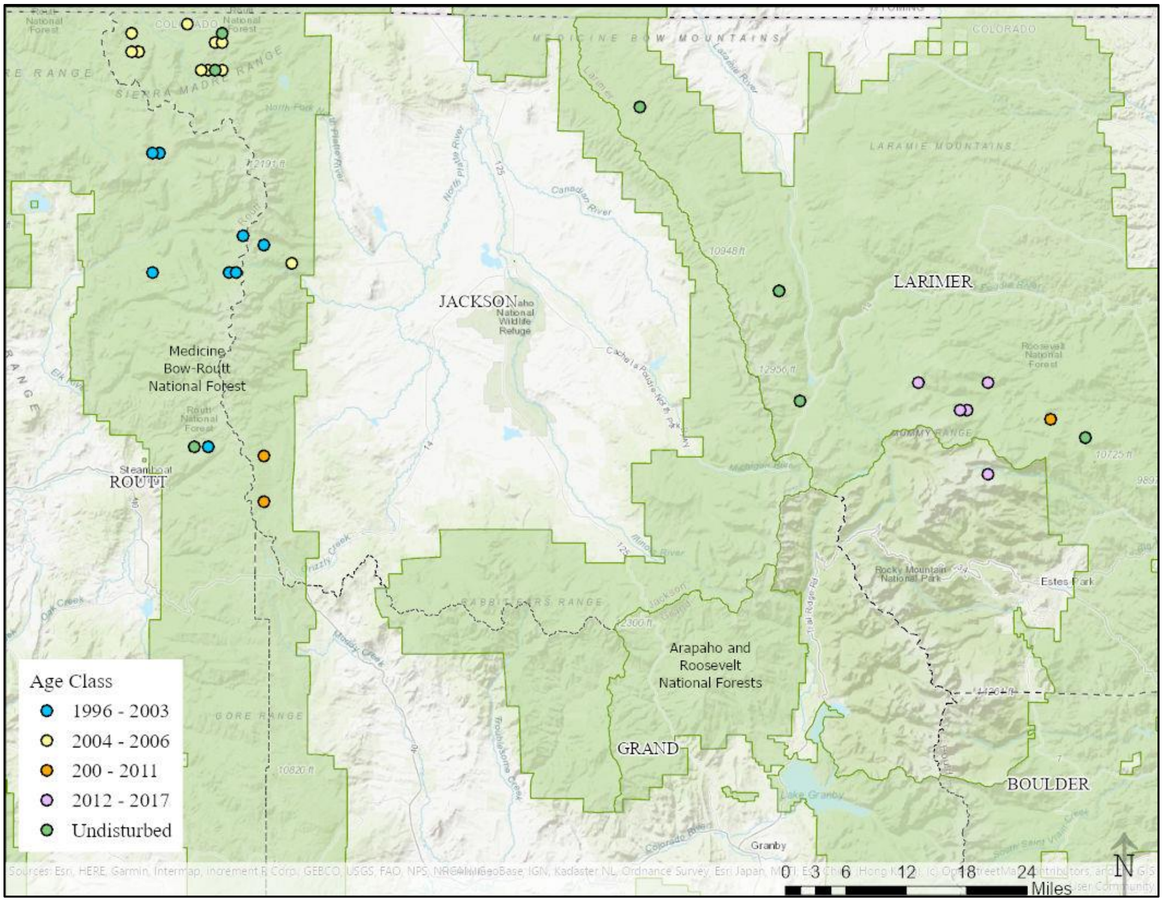

Figure 1: Map of 44 surveyed plots coded by age class; the study area includes the extent of the points within green, which is National Forest land; dashed lines indicate county boundaries.

Each plot was circular and measured 34.7 meters in diameter, in alignment with published protocols (Holt et al. 2007). If plots were inaccessible or did not meet our requirements for the study area, i.e. more than 5% snow cover, or more than 5% lodgepole or limber pine present, we relocated the center point a random direction and distance within 2 kilometers of the original plot center.

Surveys within the plots were conducted for a maximum of 2 hours and a minimum of 45 minutes; if a new species was not found after 15 minutes then the survey ended prematurely. This method was modified from Forest Inventory Assessment protocols (McCune 2000). Plot environmental characteristics were recorded visually by one member of our team using an eight-part percentage scale: < 1, 1, 5, 10, 25, 50, 75, and > 90. These environmental characteristics included bare soil/duff cover, fine and coarse woody debris cover, lichen cover on the ground/rocks, lichen cover on trees, understory cover, moss cover, overstory fir abundance, average canopy cover, average basal area, and overstory spruce abundance (Table 1). We considered fine woody debris to be woody debris less than 8 cm in diameter, and coarse woody debris as woody debris greater than 8 cm in diameter. In five locations within the plot (i.e. the center and four cardinal edges), a spherical densiometer was used to record canopy cover, and a wedge prism to record basal area. The average of these five locations was assigned to each plot as the canopy cover average or basal area average (Lists 1, 2; Table 1). Lastly, four digital pictures were taken from the center of each plot for future reference and habitat evaluation.

Presence of every vascular species was noted at each plot (or frequency across the study area) and only specimens under three meters in height were recorded. Collected vouchers were pressed in the field and then identified using a local flora (Ackerfield 2015) at the University of Northern Colorado Herbarium. Of the 1,241 vouchers collected, 1,041 (83%) were identified to some taxonomic level: species, genus, or family. Identification was limited by specimen quality and the absence of characteristic traits due to seasonal variance or decomposition of plant matter; vouchers in the *Carex* and *Poa* genera commonly lacked identifiable traits and keying every voucher to species was outside the scope of this study. Of those identified, 606 (58%) vouchers were keyed to species and only species-level identifications will be presented below unless noted otherwise.

Findings

Out of the original 44 plots surveyed, only 37 plots were used in our analysis due to the poor specimen quality of 7 plots. The primary cause of poor quality was mold that rendered collected specimen unidentifiable. We sampled 14 plots in Roosevelt National Forest and 23 plots in Routt National Forest. Of the 37 plots we used, 8 represented age class 1 (1996 – 2003), 12 represented age class 2 (2004 – 2006), 5 represented age class 3 (2007 – 2011), 5 represented age class 4 (2012 – 2011), and 7 represented age class 5 (Undisturbed; Table 1).

Table 1. Plot characteristics by age class. Numbers represent averages across all plots in that class, and numbers in parentheses are associated standard deviations.

	1: 1996 – 2003	2: 2004 – 2006	3: 2007 – 2011	4: 2012 – 2017	5: Undisturbed
No. Surveyed Plots	8	12	5	5	7
Total Acreage	7.5	11.2	4.7	4.7	6.5
Gamma Diversity	78	92	38	26	48
Alpha Diversity	21.5 (7.2)	21.3 (10.6)	13.6 (8.0)	9 (5.1)	14.3 (4.7)
Bare Soil/Duff	15.8 (10.3)	18.8 (14.0)	14.2 (10.5)	4.2 (1.8)	12.3 (9.3)
Fine Woody Debris	11.4 (9.4)	12.6 (13.1)	13 (6.7)	21 (17.5)	9.6 (10.7)
Coarse Woody Debris	26.3 (20.5)	24.16 (14)	32 (17.5)	45 (21)	19.3 (15.7)
Lichen Cover (Ground & Rocks)	6.5 (4.0)	3.5 (3.5)	8.4 (10.0)	31.2 (31.3)	5.5 (4.9)
Lichen Cover (Trees)	14.75 (25.6)	16.6 (18.4)	30.4 (32.1)	15.6 (21.9)	28.85 (26.4)
Understory Cover	72.5 (15.4)	70.8 (21.9)	84 (8.2)	69 (30.1)	79.3 (7.3)
Moss Cover	33.1 (19.3)	23.2 (21.5)	36 (27.0)	48 (37.0)	23.3 (15.7)
Subalpine Fir Abundance	72.1 (16.5)	73.2 (12.9)	73 (14.4)	70 (11.2)	70 (24.2)
Canopy Cover Average *	50.8 (14.5)	57.5 (13.8)	55.6 (8.7)	62.2 (15.9)	66.2 (9.5)

Basal Area Average *	6.8 (1.5)	8.0 (1.2)	7.2 (1.2)	6.5 (2.1)	8.5 (1.1)
Engelmann Spruce Abundance *	21.9 (14.1)	16.7 (8.9)	24 (16.4)	22 (18.6)	25 (18.7)

* Included in Lists 1, 2 as a plot variable

In total, 36 families were documented, comprising 128 species (List 1) of 606 specimens. The most frequent species, in order, were *Vaccinium scoparium* (Whortleberry), *Abies bifolia* (Subalpine fir), *Picea engelmannii* (Engelmann spruce), *Arnica cordifolia* (Heartleaf arnica), and *Chamerion angustifolium* (Fireweed; Table 2); *Vaccinium* was found in every plot we surveyed (37 plots).

Table 2. Perfect indicators of each age class (i.e. taxa found in every plot of that class). The number of species found in every plot within an age class corresponds to the written species in the last row.

1: 1996-2003	2: 2004-2006	3: 2007-2011	4: 2012-2017	5: Undisturbed
4 *Vaccinium scoparium* *Abies bifolia* *Picea engelmannii* *Chamerion angustifolium*	2 *Vaccinium scoparium* *Arnica cordifolia*	4 *Vaccinium scoparium* *Abies bifolia* *Picea engelmannii* *Chamerion angustifolium*	3 *Vaccinium scoparium* *Abies bifolia* *Picea engelmannii*	2 *Vaccinium scoparium* *Abies bifolia*

When we compiled species and environmental data across age classes, we discovered that only two species were found in every Undisturbed plot: *V. scoparium* and

A. bifolia. This age class had an average 14.3 species per plot and a gamma diversity, i.e. the number of unique species found across all Undisturbed plots, of 48. An additional two species (*P. engelmannii* and *C. angustifolium*) were found in every plot belonging to the oldest age class (1996 – 2003; Table 2). The average species diversity of these 1996 – 2003 plots was 21.5 and the age class had 78 unique species. *Vaccinium* and *Arnica cordifolia* were found at every plot affected between 2004 – 2006 and had the highest gamma diversity of 92. The alpha diversity for this age class was 21.3 and it was the only class where we found *Arnica* in every plot. The third age class (2007 – 2011) mimicked the oldest age class in terms of species, however it only had 38 unique species across all plots of this class and 13.6 species as the average alpha diversity. The most recently affected age class (2012 – 2017) had the smallest gamma and alpha diversities of 26 and 9, respectively.

The bulk of our findings are summarized into two annotated lists. The first is an annotated species list to reflect the 128 total understory vascular plants we encountered in this study (List 1). The second is an annotated plot list to summarize factors in the 37 total plots we visited in the summer of 2018 (List 2).

List 1: Annotated Species List

The arrangement of the annotated list of vascular species follows this format: the full scientific name of each species is italicized followed by its authority and one common name referenced in Ackerfield (2015). The first whole number signifies the number of plots out of 37 where the species was found, and the corresponding age classes (1 represents 1996 – 2003, 2 represents 2004 – 2006, 3 represents 2007 – 2011, 4 represents 2012 – 2017, and 5 represents Undisturbed) are indicated in square brackets.

The last three numbers are summaries across plots of Canopy cover average, Basal area average, and Spruce abundance range.

Abies bifolia A. Murray, Rocky Mountain subalpine fir; 34 [1, 2, 3, 4, 5] C: 58.7, B: 7.4, S: 5-50

Achillea millefolium L., Common yarrow; 8 [1, 2] C: 51.3, B: 7.3, S: 5-25

Aconitum columbianum Nutt., Columbian monkshood; 4 [1, 2, 3] C: 56.2, B: 7.1, S: 10-25

Anaphalis margaritacea (L.) Benth. & Hook., Pearly everlasting; 7 [1, 2] C: 56.8, B: 7.3, S: 10-50

Antennaria anaphaloides Rydb., Pearly pussy-toes; 1 [1] C: 48.4, B: 4.2, S: 25

Antennaria corymbosa E.E. Nelson, Flat-top pussy-toes; 1 [2] C: 43.6, B: 5.8, S: 25

Antennaria parvifolia Nutt., Small-leaf pussy-toes; 2 [1, 2] C: 45.1, B: 6.9, S: 10-25

Antennaria pulcherrima (Hook.) Greene, Showy pussy-toes; 2 [2, 5] C: 60.2, B: 8.7, S: 10-50

Antennaria rosea Greene, Rosy pussy-toes; 8 [1, 2, 3, 4] C: 41.1, B: 6.7, S: 5-25

Antennaria umbrinella Rydb., Umber pussy-toes; 5 [1, 2, 3, 4] C: 38.7, B: 5.6, S: 10-50

Aquilegia coerulea James, Colorado blue columbine; 1 [1, 5] C: 69.1, B: 7.8, S: 5-25

Arabis pycnocarpa M. Hopkins var. *pycnocarpa,* Hairy rockcress; 8 [1, 2, 4, 5] C: 50.3, B: 6.7, S: 5-50

Arctostaphylos uva-ursi (L.) Spreng., Kinnikinnick; 3 [2, 4, 5] C: 65.6, B: 7.5, S: 10-25

Arnica cordifolia Hook., Heartleaf arnica; 31 [1, 2, 3, 4, 5] C: 58.4, B: 7.6, S: 5-50

Arnica latifolia Bong., Broadleaf arnica; 3 [2] C: 58.2, B: 8.3, S: 10-25

Arnica mollis Hook., Hairy arnica; 1 [2] C: 74.2, B: 8.7, S: 10

Arnica parryi A.Gray, Parry's arnica; 2 [1] C: 47.8, B: 6.2, S: 10-25

Artemisia cana Pursh, Hoary sagebrush; 1 [1] C: 48.4, B: 4.2, S: 25

Berberis repens Lindl., Oregon-grape; 5 [1, 2, 4, 5] C: 59.5, B: 7, S: 5-25

Besseya alpina (A. Gray) Rydb., Alpine kittentails; 2 [1, 5] C: 65.3, B: 8.8, S: 5-25

Bistorta bistortoides (Pursh) Small, American bistort; 4 [1, 3, 5] C: 56.4, B: 7.7, S: 5-25

Caltha leptosepala DC., Marsh marigold; 3 [1, 2] C: 67.9, B: 7.8, S: 5-25

Campanula rotundifolia L., Bluebells of Scotland; 1 [2] C: 43.4, B: 6.7, S: 10

Capsella bursa-pastoris (L.) Medik., Shepherd's purse; 7 [1, 2, 3] C: 48.4, B: 6.7, S: 10-25

Cardamine cordifolia A. Gray, Heartleaf bittercress; 1 [1] C: 56.6, B: 7.2, S: 25

Carex ebenea Rydb., Ebody sedge; 2 [2] C: 48.1, B: 8.5, S: 25

Carex micropoda C.A. Mey., Pyrenean sedge; 1 [1] C: 46.6, B: 8.1, S: 10

Carex nebrascensis Dewey, Nebraska sedge; 2 [2] C: 58.9, B: 7.2, S: 10-25

Castilleja miniata Dougl. ex Hook., Red Indian paintbrush; 5 [1, 2, 5] C: 52.1, B: 6.6, S: 10-25

Castilleja rhexifolia Rydb., Splitleaf Indian paintbrush; 1 [3] C: 50.4, B: 7, S: 10

Chamerion angustifolium (L.) Holub, Fireweed; 30 [1, 2, 3, 4, 5] C: 58.9, B: 7.6, S: 5-50

Chimaphila umbellata (L.) W.P.C. Barton, Pipsissewa; 4 [1, 4, 5] C: 65.6, B: 7, S: 10-25

Cirsium arvense (L.) Scop., Canada thistle; 3 [1, 2] C: 54.3, B: 6.4, S: 10-25

Cirsium ochrocentrum A. Gray, Yellowspine thistle; 1 [2] C: 41.8, B: 6.9, S: 25

Cirsium scariosum Nutt., Elk thistle; 1 [2] C: 43.4, B: 6.7, S: 10

Corallorhiza maculata (Raf.) Raf., Spotted coralroot; 1 [5] C: 72.4, B: 7.3, S: 25

Corallorhiza striata Lindl., Striped coralroot; 5 [2, 5] C: 58.7, B: 8.2, S: 5-25

Cypripedium fasciculatum Kellogg ex S. Watson, Purple lady's slipper; 1 [2] C: 71, B: 9.4, S: 10

Delphinium barbeyi (Huth) Huth, Subalpine larkspur; 1 [3] C: 50.4, B: 7, S: 10

Draba albertina Greene, Slender draba; 1 [2] C: 58.6, B: 9.4, S: 25

Draba nemorosa L., Woodland draba; 1 [2] C: 37.6, B: 7.6, S: 25

Epilobium halleanum Hausskn., Glandular willow-herb; 2 [2, 5] C: 74.1, B: 9.5, S: 5-10

Epilobium hornemannii Rchb. var. *hornemannii*, Hornemann's willow-herb; 8 [1, 2] C: 51.4, B: 7.9, S: 10-25

Epilobium lactiflorum Hausskn., Milkflower willowherb; 8 [1, 2, 3, 5] C: 60.2, B: 7.4, S: 5-25

Equisetum arvense L., Field horsetail; 1 [2] C: 73, B: 7.7, S: 5

Eremogone congesta var. *congesta* (Nutt.) Ikonn., Ballhead sandwort; 1 [5] C: 49.4, B: 8.1, S: 50

Erigeron coulteri Porter, Coulter's daisy; 2 [1, 2] C: 46.9, B: 6.7, S: 10-25

Erigeron elatior (Gray) Greene, Tall daisy; 1 [3] C: 50.4, B: 7, S: 10

Erigeron eximius Greene, Splendid daisy; 1 [2] C: 74.2, B: 8.7, S: 10

Erythronium grandiflorum Pursh ssp. *grandiflorum*, Avalanche lily; 14 [1, 2, 3, 5] C: 49.4, B: 7.1, S: 10-50

Fragaria virginiana Mill, Mountain strawberry; 7 [1, 2, 4, 5] C: 62.4, B: 6.9, S: 5-25

Galium boreale L., Northern bedstraw; 3 [1, 2] C: 59.8, B: 7, S: 10-25

Gayophytum diffusum Torr. & A. Gray ssp. *parviflorum* F.H. Lewis & Szweyk., Diffuse groundsmoke; 1 [1] C: 48.4, B: 4.2, S: 25

Gentiana parryi Engelm., Parry's gentian; 5 [2, 3, 5] C: 54.3, B: 7.6, S: 10-50

Geranium bicknellii Britton, Bicknell's cranesbill; 1 [2] C: 37.6, B: 7.6, S: 25

Geranium richardsonii Fisch. & Trautv., Richardson's geranium; 9 [1, 2, 3, 5] C: 55.6, B: 6.9, S: 10-25

Goodyera oblongifolia Raf., Western rattlesnake plantain; 1 [5] C: 62.8, B: 7.7, S: 10

Heterotheca pumila (Greene) Semple, Alpine false goldenaster; 2 [1] C: 52.5, B: 5.7, S: 25

Hieracium albiflorum Hook., White hawkweed; 14 [1, 2, 3, 4, 5] C: 56.3, B: 7.4, S: 5-50

Hieracium fendleri Sch. Bip., Yellow hawkweed; 4 [2, 3, 5] C: 65, B: 8.5, S: 5-25

Hieracium triste Willd. ex Spreng., Slender hawkweed; 1 [1] C: 47.2, B: 8.2, S: 10

Juncus drummondii E. Mey., Drummond's rush; 2 [2] C: 65.8, B: 8.5, S: 5-25

Juncus parryi Engelm., Parry's rush; 6 [1, 2, 3] C: 53.5, B: 7.2, S: 5-25

Juniperus communis L. var. *depressa* Pursh, Common juniper; 12 [2, 3, 4, 5] C: 59.3, B: 7.2, S: 5-50

Lathyrus lanszwertii Kellogg var. *leucanthus* (Rydb.) Dorn, Lanszwert's pea; 1 [3] C: 50.4, B: 7, S: 10

Ligusticum porteri J.M. Coult. & Rose, Osha; 1 [1] C: 62.2, B: 7.6, S: 50

Linnaea borealis L. var. *longiflora* Torr., Twinflower; 1 [2] C: 43.6, B: 5.8, S: 25

Listera cordata (L.) R. Br. ex Ait. F. var. *nephrophylla* (Rydb.) Hultén, Heartleaf twayblade; 10 [1, 2, 3, 5] C: 57, B: 7.5, S: 5-25

Lonicera involucrata (Richardson) Banks ex Spreng., Black twinberry; 1 [2] C: 43.6, B: 5.8, S: 25

Lupinus argenteus Pursh var. *argenteus*, Silvery lupine; 2 [1] C: 55.3, B: 5.9, S: 25-50

Luzula parviflora (Ehrh.) Desv., Small-flowered woodrush; 6 [1, 2, 5] C: 62.3, B: 8.6, S: 5-50

Mertensia ciliata (James ex Torr.) G. Don, Streamside bluebells; 9 [1, 2, 3] C: 54.6, B: 7.6, S: 5-50

Mitella pentandra Hook., Five-star mitrewort; 8 [1, 2, 3, 5] C: 63.8, B: 8.1, S: 5-25

Musineon divaricatum (Pursh) Raf., Leafy wildparsley; 1 [5] C: 59.8, B: 8, S: 25

Orobanche fasciculata Nutt., Clustered broomrape; 1 [1] C: 61.7, B: 6.5, S: 25

Osmorhiza berteroi DC., Sweet-cicely; 1 [2] C: 74.2, B: 8.7, S: 10

Osmorhiza depauperata Phil., Blunt sweet-cicely; 3 [1, 2] C: 59.7, B: 8.6, S: 10-25

Oxypolis fendleri (A. Gray) Heller, Fendler's cowbane; 1 [3] C: 50.4, B: 7, S: 10

Packera fendleri (Gray) W.A. Weber & A. Löve, Fendler's ragwort; 9 [1, 2, 3, 5] C: 55.9, B: 7.7, S: 5-50

Paxistima myrsinites (Pursh) Raf., Oregon boxleaf; 1 [1] C: 62.2, B: 7.6, S: 50

Pedicularis bracteosa Benth. var. *paysoniana* (Pennell) Cronquist, Payson's lousewort; 1 [5] C: 59.8, B: 8, S: 25

Pedicularis groenlandica Retz., Elephant's head; 3 [1, 2] C: 58.1, B: 7.2, S: 10-25

Pedicularis racemosa Douglas ex Benth. var. *alba* Pennell, Sickletop lousewort; 17 [1, 2, 3, 5] C: 57.6, B: 7.9, S: 5-25

Penstemon whippleanus A. Gray, Whipple's penstemon; 10 [1, 2, 3, 5] C: 49.2, B: 7, S: 5-25

Picea engelmannii Parry ex Engelm. var. *engelmannii*, Englemann spruce; 32 [1, 2, 3, 4, 5] C: 59.1, B: 7.4, S: 5-50

Pinus contorta Douglas ex Loud. var. *latifolia* Engelm., Lodgepole pine; 6 [1, 2, 4, 5] C: 61.3, B: 7.7, S: 5-50

Pinus flexilis E. James, Limber pine; 1 [2] C: 43.4, B: 6.7, S: 10

Platanthera dilatata (Pursh) Lindley ex L.C. Beck var. *albiflora* (Cham.) Ledeb., Scentbottle; 1 [1, 2, 3] C: 58, B: 7.2, S: 10-50

Platanthera purpurascens (Rydb.) Sheviak & W.F. Jennings, Purple-petal bog orchid; 5 [2] C: 73.6, B: 8.2, S: 5-10

Polemonium pulcherrimum Hook. Ssp. *delicatum* (Rydb.) Cronquist, Jacob's ladder; 1 [1, 2, 3, 4, 5] C: 51.2, B: 7, S: 5-50

Populus tremuloides Michx., Quaking aspen; 13 [1, 2, 4] C: 60.8, B: 7.3, S: 5-25

Potentilla gracilis Douglas ex Hook. var. *elmeri* (Rydb.) Jeps., Slender cinquefoil; 5 [1] C: 48.4, B: 4.2, S: 25

Potentilla hippiana Lehm. var. *hippiana*, Woolly cinquefoil; 1 [2] C: 43.4, B: 6.7, S: 10

Pterospora andromedea Nutt., Pinedrops; 1 [1, 5] C: 65.3, B: 7.5, S: 10-25

Pyrola minor L., Lesser wintergreen; 2 [1, 2, 3, 4, 5] C: 65.4, B: 8, S: 5-50

Ranunculus uncinatus D. Don ex G. Don, Woodland buttercup; 10 [2, 3] C: 56.5, B: 8, S: 10-25

Rhododendron albiflorum Hook., White azalea; 3 [1] C: 47.2, B: 8.2, S: 10

Rhodiola rhodantha (A. Gray) Jacobsen, Rose crown; 1 [1] C: 56.6, B: 7.2, S: 25

Ribes coloradense Coville, Colorado current; 1 [1] C: 56.6, B: 7.2, S: 25

Ribes lacustre (Pers.) Poir., Prickly currant; 1 [2, 4] C: 56.9, B: 6, S: 25

Rorippa palustris (L.) Besser, Bog yellow-cress; 2 [2] C: 71, B: 9.4, S: 10

Rosa acicularis Lindl. ssp. *sayi* (Schwein.) W.H. Lewis, Prickly rose; 1 [1, 2, 4, 5] C: 56.8, B: 8.1, S: 5-50

Rosa arkansana Porter, Prairie rose; 13 [1, 2] C: 52.5, B: 6.6, S: 10-25

Rosa woodsii Lindl., Wood's rose; 2 [1, 2] C: 52.6, B: 6.1, S: 25

Rubus parviflorus Nutt. var. *parviflorus*, Thimbleberry; 2 [1, 2, 5] C: 62.4, B: 7.7, S: 5-25

Rubus idaeus L. var. *strigosus* (Michx.) Maxim., Red raspberry; 4 [1, 2, 3, 4, 5] C: 55, B: 7, S: 5-50

Sambucus racemosa L. var. *microbotrys* (Rydb.) Kearney & Peebles, Red elderberry; 5 [1, 2, 5] C: 53.5, B: 6.9, S: 10-50

Saxifraga bronchialis L var. *austromontana* (Wiegand) Piper, Spotted saxifrage; 5 [1, 2, 4, 5] C: 45.1, B: 7.1, S: 5-50

Sedum lanceolatum Torr., Spearleaf stonecrop; 4 [2, 4] C: 44.1, B: 6.3, S: 5-50

Senecio atratus Greene, Tall blacktip ragwort; 1 [2] C: 71, B: 9.4, S: 10

Senecio bigelovii A. Gray var. *hallii*, Hall's ragwort; 1 [5] C: 49.4, B: 8.1, S: 50

Senecio eremophilus Richardson var. *kingii* (Rydb.) Greenm., Cut-leaved groundsel; 5 [1, 2] C: 45, B: 7.2, S: 5-25

Senecio integerrimus Nutt., Lambs-tongue ragwort; 6 [1, 2] C: 54, B: 7.7, S: 5-25

Senecio triangularis Hook., Arrowleaf ragwort; 14 [1, 2, 3, 5] C: 57.3, B: 7.8, S: 5-50

Shepherdia canadensis Nutt., Canadian buffaloberry; 2 [1, 4] C: 66.8, B: 5.8, S: 25

Sibbaldia procumbens L., Creeping sibbaldia; 8 [1, 2, 4, 5] C: 50.9, B: 7.2, S: 10-50

Solidago multiradiata Ait. var. *scopulorum* A. Gray, Rocky Mountain goldenrod; 1 [5] C: 49.4, B: 8.1, S: 50

Solidago simplex Kunth var. *simplex*, Mt. Albert goldenrod; 2 [1, 2] C: 51.7, B: 6.7, S: 25

Streptopus amplexifolius (L.) DC., Claspleaf twisted stalk; 7 [1, 2, 3] C: 58.2, B: 7.6, S: 5-25

Symphyotrichum ascendens (Lindl.) G.L. Nesom, Western aster; 17 [1, 2, 3, 5] C: 52.3, B: 7.1, S: 10-50

Symphyotrichum foliaceum (DC.) G.L. Nelsom var. *parryi* (D.C. Eaton) G.L. Nesom, Parry's aster; 5 [1, 2, 5] C: 47, B: 6.7, S: 10-50

Taraxacum officinale F.H. Wigg., Common dandelion; 2 [2] C: 54.3, B: 8.5, S: 10-25

Trillium ovatum Pursh ssp. *ovatum*, Pacific trillium; 2 [2] C: 58.9, B: 7.2, S: 10-25

Trollius albiflorus (A. Gray) Rydb., White globeflower; 3 [3, 5] C: 55, B: 8, S: 10-25

Vaccinium scoparium Leiberg ex Coville, Dwarf red whortleberry; 37 [1, 2, 3, 4, 5] C: 58.5, B: 7.5, S: 5-50

Vicia americana Muhl. ex Willd. var. *americana*, American vetch; 1 [1] C: 48.4, B: 4.2, S: 25

Zigadenus elegans Pursh, Mountain death camas; 6 [2, 4, 5] C: 68.8, B: 7.7, S: 5-25

List 2: Annotated Plot List

The arrangement of the annotated plot list follows this format: the name of each plot is first denoted with the capital letter G (group, or age class) and then the age class (1 represents 1996 – 2003, 2 represents 2004 – 2006, 3 represents 2007 – 2011, 4 represents 2012 – 2017, and 5 represents Undisturbed), the plot ID is denoted with capital letter P (plot) and then a two digit number. Next, we note the forest, i.e., Routt NF or Roosevelt NF, in which the plot was located. This name is followed by the number of unique understory species identified within the plot, as well as the slope (degrees) and elevation (feet) recorded in the center of each plot. Slopes that were not recorded are signified by a dash “-”. The last three variables: C, B, and S, report the plot’s Canopy cover average, Basal area average, and Spruce abundance, respectively.

G1_P01, Routt; 27 (3°, 9368 ft) C: 48.4, B: 4.2, S: 25

G1_P10, Routt; 21 (14°, 10284 ft) C: 47.2, B: 8.2, S: 10

G1_P11, Routt; 34 (16°, 10003 ft) C: 56.6, B: 7.2, S: 25

G1_P12, Routt; 18 (21°, 9641 ft) C: 62.2, B: 7.6, S: 50

G1_P13, Routt; 23 (25°, 8978 ft) C: 61.7, B: 6.5, S: 25

G1_P15, Routt; 9 (30°, 9854 ft) C: 64.4, B: 7.6, S: 5

G1_P16, Routt; 21 (14°, 10667 ft) C: 46.6, B: 8.1, S: 10

G1_P19, Routt; 19 (8°, 11014 ft) C: 19.6, B: 4.8, S: 25

G2_P02, Routt; 21 (31°, 10241 ft) C: 41.8, B: 6.9, S: 25

G2_P03, Roosevelt; 15 (10°, 9533 ft) C: 73, B: 7.7, S: 5

G2_P05, Routt; 11 (13°, 10207 ft) C: 74, B: 8.5, S: 25

G2_P06, Routt; 27 (32°, 10108 ft) C: 43.4, B: 6.7, S: 10

G2_P07, Routt; 37 (-°, 8894 ft) C: 74.2, B: 8.7, S: 10

G2_P08, Routt; 14 (-°, 9907 ft) C: 51.8, B: 8.2, S: 5

G2_P09, Roosevelt; 4 (13°, 10332 ft) C: 56.2, B: 7.6, S: 25

G2_P11, Routt; 38 (8°, 9122 ft) C: 43.6, B: 5.8, S: 25

G2_P12, Routt; 28 (12°, 10368 ft) C: 37.6, B: 7.6, S: 25

G2_P13, Routt; 11 (12°, 9272 ft) C: 65.2, B: 9.6, S: 10

G2_P16, Routt; 23 (0°, 10052 ft) C: 58.6, B: 9.4, S: 25

G2_P20, Routt; 26 (8°, 9499 ft) C: 71, B: 9.4, S: 10

G3_P01, Roosevelt; 9 (21°, 10197 ft) C: 69.6, B: 7.1, S: 50

G3_P04, Routt; 17 (10°, 9130 ft) C: 46.6, B: 5.6, S: 25

G3_P05, Routt; 26 (16°, 9617 ft) C: 50.4, B: 7, S: 10

G3_P09, Roosevelt; 10 (27°, 10264 ft) C: 55, B: 9, S: 25

G3_P12, Roosevelt; 6 (25°, 9184 ft) C: 56.4, B: 7.4, S: 10

G4_P02, Roosevelt; 17 (35°, 9770 ft) C: 72, B: 5.1, S: 25

G4_P05, Roosevelt; 7 (19°, 9675 ft) C: 66.8, B: 7.6, S: 5

G4_P06, Roosevelt; 8 (15°, 10063 ft) C: 46.6, B: 3.5, S: 50

G4_P11, Roosevelt; 10 (23°, 10090 ft) C: 44.6, B: 8.3, S: 5

G4_P19, Roosevelt; 3 (31°, 10206 ft) C: 80.8, B: 7.8, S: 25

G5_P01, Roosevelt; 11 (9°, 10178 ft) C: 62.8, B: 7.7, S: 10

G5_P02, Routt; 18 (10°, 9910 ft) C: 74, B: 10.4, S: 5

G5_P03, Roosevelt; 17 (22°, 10128 ft) C: 59.8, B: 8, S: 25

G5_P17, Routt; 18 (11°, 10107 ft) C: 49.4, B: 8.1, S: 50

G5_P18, Routt; 18 (19°, 9529 ft) C: 72.4, B: 7.3, S: 25

G5_P19, Roosevelt; 6 (33°, 10232 ft) C: 76, B: 9.7, S: 50

G5_P20, Roosevelt; 12 (43°, 9925 ft) C: 69, B: 8.6, S10

Discussion

Slight differences in understory composition were noted in each age class, however there are some notable patterns. The youngest age class has the lowest alpha, 9, and gamma diversity, 26, as well as the smallest average basal area and the greatest cover of bare soil/duff, woody debris, and lichen ground cover (Table 1). This overall lower density we observed aligns with previous observations of slow turnover in early-seral communities (Winter et al. 2015). Conversely, the second-oldest age class (2004-2006) had the highest gamma diversity and lowest overstory spruce cover. This exceptional diversity may be a result of unequal sample size, as the number of plots surveyed within this age class were greater than all the others, leading to greater representation in the data. On the other hand, it may be that understory vascular plants generally peak in diversity 14 to 16 years after an outbreak (corresponding to plots infested 2004 – 2006), after which the community begins to progress toward its original state. This aligns with our data as the oldest age class had greater spruce cover than this second-oldest plot and lower gamma diversity. Other research has found a similar trajectory of diversity following beetle disturbance, but the successional timeline was more protracted, i.e., maximal diversity occurred after 25 years (Winter et al. 2015).

The original overstory characteristics of a plot may also have a large impact on future understory growth as suggested in Boucher and Mead (2006), who found large variance between beetle-affected plots in different geographic regions of the Kenai Peninsula, AK. These subtle patterns make our research valuable to the literature and future research of understory growth changes after a spruce beetle disturbance. We recommend conducting similar studies to create a timeline of succession and change in the subalpine forests of northern Colorado.

As noted in Zorio et al. (2016), *Vaccinium* is among the most common groundcover in spruce-fir forests. Presence of *Vaccinium* was recorded in every plot (37) we visited and was often a visual indicator of spruce-fir forest type as we approached the plots. Subalpine fir, as saplings, was the next most abundant species found in 34 plots; the only age class where it was not found in all plots was 2004 – 2006. Spruce saplings below 3 meters were also absent from two plots in age class 2 (2004 – 2006) and three plots in age class 5 (Undisturbed); spruce saplings below 3 meters were recorded in 32 plots. The high frequency of these two tree species as understory saplings aligns with Veblen et al. (1991) who noted that following the death of mature trees, smaller diameter trees of both species proliferated with similarly high growth rates exceeding the next 40 years in areas with severe outbreak. Veblen et al. (1991) predicted that fir trees would grow more quickly due to their high abundance in subalpine forests, however spruces will eventually reach pre-outbreak levels due to their longevity and sturdiness.

Arnica cordifolia was the next most abundant species with presence recorded in 31 plots, which also aligns with observations made by Zorio et al. (2016) in subalpine forests of the Rocky Mountains. The fifth most abundant species was *Chamerion* *angustifolium*, or fireweed, recorded in 30 sites. Fireweed seedlings often appear after forest disturbances, particularly fire and clearcutting (Romme et al. 1995, Kreyling et al. 2008a), so it surprised us that its frequency among the most recently disturbed plots was relatively low. Both forbs appear to be least prevalent in our most recently disturbed sites (2012 – 2017), although were the fourth and fifth most frequent taxa in our study.

While our five most common species were prevalent throughout the study area regardless of canopy characteristics, we can derive information about the understory from the next-most common species (Table 3). In plots with the highest canopy cover averages, the common species recorded (excluding the five most common) align with those found in dense coniferous forests, for example *Mitella pentandra* which flourishes in shaded, moist spots (Table 3). In contrast, the species found in plots with the lowest canopy cover align with those often found in open and sunny areas, such as *Antennaria rosea* and *Pedicularis racemosa* (Table 3). These subtle indications of understory composition serve as important insights to the future regeneration of subalpine forests and early-seral stage communities after a spruce beetle outbreak.

Table 3. Comparison of most frequent species between ten plots with the highest canopy cover averages and ten plots with the lowest canopy cover averages. We list the species' presence in these plots, the highest value a species can have is ten. Shaded rows indicate the species common to both groups of plots.

Highest Canopy Cover		Lowest Canopy Cover	
Vaccinium scoparium	10	*Vaccinium scoparium*	10
Abies bifolia	10	*Picea engelmannii*	9
Picea engelmannii	9	*Abies bifolia*	9
Arnica cordifolia	8	*Arnica cordifolia*	9
Chamerion angustifolium	8	*Chamerion angustifolium*	7
Senecio triangularis	5	*Symphyotrichum ascendens*	7
Fragaria virginiana	4	*Antennaria rosea*	7
Hieracium albiflorum	4	*Erythronium grandiflorum*	6
Juniperus communis	4	*Pedicularis racemosa*	6
Mitella pentandra	4	*Hieracium albiflorum*	5

The canopy cover averages across age classes ranged from 50.8% (1996 – 2003) to 66.2% (Undisturbed) and associated variance was large leading us to conclude that the age classes are not ecologically different. Average basal area follows a similar trend with a range from 6.5 (2012 – 2017) up to 8.5 (Undisturbed). These trends somewhat match our hypothesis as canopy cover and basal area were expected to be high in Undisturbed sites, however the range of values is not wide enough, nor the variance within classes narrow enough, to clearly derive a pattern between spruce beetle disturbance and understory growth and diversification. Most interestingly, average overstory spruce abundance was relatively similar across age classes as well. Our recorded abundance ranged from 16.7% (2004 – 2006) up to 25% (Undisturbed). This somewhat contradicts our assumption that decreasing spruce abundance would release light and nutrients to the understory and may be a result of previous plot characteristics which favored spruce persistence in the face of disturbance. Boucher and Mead's (2006) work with spruce beetle outbreaks in the white spruce forests of the Kenai Peninsula, Alaska revealed high variability between geographically distinct plots and they noticed spruce regeneration in almost all areas of disturbance.

When accounting for all specimens we collected during this study, the most well-represented families throughout the study area were Ericaceae and Pinaceae. Species from these two families were found in all 37 plots, most likely due to the prevalence of *Vaccinium*, Subalpine fir, and Engelmann spruce. Asteraceae and Cyperaceae were the next most common families with each found in 34 plots. The most common Asteraceae species were *Arnica cordifolia*, *Symphyotrichum ascendens,* and *Hieracium albiflorum* while the most common Cyperaceae species were in the genus *Carex*. Our fifth most common family was Poaceae, however none of the collected specimens of this family were keyed to species.

Conclusion

We set out to find patterns in the years following a spruce beetle disturbance and found that the understory community's gamma and alpha diversity increased with time since the outbreak. Our results provide a brief (21 years) look at shifts in the understory vascular plant community towards higher overall species diversity with time. In accordance with the literature, we conclude that these patterns occur from the slow fall of tree needles leading to an evolving, open canopy site (Holsten et al. 1999, Winter et al. 2015). The youngest age class had the lowest species diversity and highest spruce cover while the oldest age class had the highest diversity with the lowest spruce cover.

At the same time, more observation is necessary to understand the complete effect of spruce beetle disturbance in the northern Colorado Rocky Mountains. Warming temperatures and increasingly severe storms may heighten these effects in the future (), so we highly recommend the continued study of spruce beetle disturbance in subalpine forests across Colorado.

References

Ackerfield, J. (2015). Flora of Colorado. BRIT Press. Fort Worth, Texas, US.

Bentz, B.J. and K. Klepzig. (2014). Bark beetles and climate change in the United States. USDA Forest Service Climate Change Resource Center. http://www.fs.usda.gov/ccrc/topics/insectdisturbance/bark-beetles. Accessed July 12, 2019.

Bentz, B. J., Régnière, J., Fettig, C. J., Hansen, E. M., Hayes, J. L., Hicke, J. A., Kelsey, R. G., Negrón, J. F., & Seybold, S. J. (2010). Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience, 60(8), 602-613.s

Boucher, T. V., & Mead, B. R. (2006). Vegetation change and forest regeneration on the Kenai Peninsula, Alaska following a spruce beetle outbreak, 1987–2000. Forest Ecology and Management, 227(3), 233-246.

Colorado Department of Natural Resources & Colorado State University (2018). The 2018 Report on the Health of Colorado's Forests.

Colorado State Forest Service (CSFS) & U.S. Forest Service Rocky Mountain Region (1996 – 2017). Aerial Detection Survey.

DeRose, R. J., & Long, J. N. (2012). Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest. Canadian Journal of Forest Research, 42(9), 1649-1660.

Fornwalt, P. J., Rhoades, C. C., Hubbard, R. M., Harris, R. L., Faist, A. M., & Bowman, W. D. (2018). Short-term understory plant community responses to salvage logging in beetle-affected lodgepole pine forests. Forest Ecology and Management, 409, 84-93.

Hart, S. J., Veblen, T. T., Eisenhart, K. S., Jarvis, D., & Kulakowski, D. (2014). Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. Ecology, 95(4), 930-939.

Holsten, E. H., Their, R. W., Munson, A. S., & Gibson, K. E. (1999). The spruce beetle. The Bark Beetles, Fuels, and Fire Bibliography, 7.

Holt, E. A., McCune, B., & Neitlich, P. (2007). Succession and community gradients of arctic macrolichens and their relation to substrate, topography, and rockiness. North American Fungi, 2, 1-21.

Kreyling, J., Schmiedinger, A., Macdonald, E., & Beiekuhnlein, C. (2008a). Potentials of natural tree regeneration after clearcutting in subalpine forests. Western Journal of Applied Forestry, 23(1), 46-52.

Kreyling, J., Schmiedinger, A., Macdonald, E., & Beierkuhnlein, C. (2008b). Slow understory redevelopment after clearcutting in high mountain forests. Biodiversity and conservation, 17(10), 2339.

McCune, B. 2000. Lichen communities as indicator of forest health. The Bryologist 103: 353-356.

Romme, W. H., Bohland, L., Persichetty, C., & Caruso, T. (1995). Germination ecology of some common forest herbs in Yellowstone National Park, Wyoming, USA. Arctic and Alpine Research, 27(4), 407-412.

Schebeck, M., Hansen, E. M., Schopf, A., Ragland, G. J., Stauffer, C., & Bentz, B. J. (2017). Diapause and overwintering of two spruce bark beetle species. Physiological entomology, 42(3), 200-210.

Veblen, T. T., Hadley, K. S., Reid, M. S., & Rebertus, A. J. (1991). The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology, 72(1), 213-231.

Winter, M. B., Ammer, C., Baier, R., Donato, D. C., Seibold, S., & Müller, J. (2015). Multi-taxon alpha diversity following bark beetle disturbance: evaluating multi-decade persistence of a diverse early-seral phase. Forest Ecology and Management, 338, 32-45.

Zorio, S. D., Williams, C. F., & Aho, K. A. (2016). Sixty-five years of change in montane plant communities in western Colorado, USA. Arctic, Antarctic, and Alpine Research, 48(4), 703-722.